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The first discovery of crinoids and cephalopod hooklets in the British Triassic

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ABSTRACT

The Late Triassic Rhaetian stage is perhaps best known in south-west Britain for the bone beds of the Westbury Formation, but there are other fossil-rich horizons within this and the underlying Blue Anchor Formation. Samples from a borehole drilled at the Filton West Chord, and collected from exposures near Bristol Parkway railway station, have yielded significant fossil material from both of these formations. The assemblage recovered from the Blue Anchor Formation is similar to those from the lower Westbury Formation, yielding roughly equal proportions of chondrichthyans and osteichthyans. Assemblages recovered from the Westbury Formation are typical of those from the upper Westbury Formation, in being dominated by osteichthyans. The borehole samples have produced the first recorded evidence of crinoids in the British Triassic, and the first evidence of coleoid cephalopods, in

the form of grasping hooklets, from the Rhaetian, and indeed the first from the British Triassic.

Keywords: Chondrichthyes; Actinopterygii; Bristol; Rhaetian; Rhaetian bone bed; Westbury Formation; Blue Anchor Formation; cephalopod hooklets; crinoids.

1. Introduction

The Rhaetian is the short (205.7–201.3 Ma; Maron et al., 2015) final stage of the Triassic. It was a time of significant environmental change marked by a marine regression-transgression couplet that extended over much of Europe, including Britain (Hallam, 1997), and culminating in the end-Triassic mass extinction. In Britain, the Rhaetian stage corresponds to the Penarth Group, which outcrops throughout SW England, and is especially well exposed in the Severn estuary area. It overlies the Blue Anchor Formation, the uppermost unit of the Mercia Mudstone Group.

The fossil vertebrates of the British Penarth Group are well documented (e.g. Swift and Martill, 1999; Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Lakin et al., 2016), but elements of the accompanying invertebrate fauna are less well known. In particular, as Swift (1999, p. 180) noted, ‘Cephalopods are almost unknown from the Penarth Group’. He could cite only a single small ammonite, a psiloceratid, reported from Hampstead Farm Quarry, Chipping Sodbury by Donovan et al. (1989), although this record has been queried by Hodges (1994) as potentially coming from higher beds. The near absence of cephalopods in the Penarth Group is most unusual in a Mesozoic marine unit, and especially in light of the relative abundance and diversity of cephalopods throughout the marine Triassic and Jurassic in general. Much of the Penarth Group also lacks other stenohaline organisms, such as brachiopods and most echinoderms. Ophiuroids are present, but they are confined to

quite specific horizons and, in any case, are relatively euryhaline compared with other echinoderms. Together these absent taxa suggest that the Penarth Group may have been quasi-marine (slightly brackish or hypersaline) with fully marine taxa excluded.

Here we describe new discoveries of cephalopod specimens from the British Rhaetian, associated with microvertebrate remains of sharks and bony fishes and with other invertebrates. In addition, we also present an unusual occurrence of a 'Rhaetian-type bone bed' in the uppermost part of the Blue Anchor Formation, below the base of the Penarth Group. These fossils are from boreholes and from surface sampling of Penarth Group outcrops around Stoke Gifford, to the north-east of Bristol (Fig. 1). The boreholes were drilled in 2008 by Geotechnical Engineering Ltd, and sampled by Mike Curtis, a local geologist. These samples are now part of the Mike Curtis collection held by the University of Bristol School of Earth Sciences (BRSUG), which was donated to the University following his death in 2009. Additional material was collected by the authors at an outcrop of the Westbury Formation at Stoke Gifford, near Bristol Parkway railway station, in the Summer of 2015.

2. Geological Setting

The material included in this study came from two closely spaced horizons; one in the Blue Anchor Formation and one in the overlying Westbury Formation. The discovery of a bone bed near the top of the Blue Anchor Formation was unexpected, as bone beds in the Late Triassic around Bristol and the Severn are generally Rhaetian, with the most prolific being the basal bone bed of the Westbury Formation.

The Blue Anchor Formation (Warrington and Whitaker, 1984) includes sequences formerly known as the Grey Marls, the Tea Green Marls, and most of the Sully Beds. It comprises two members – the Rydon Member and the overlying Williton Member. The

Rydon Member consists of a series of dolomitic mudstones, sometimes with desiccation cracks, gypsum and rare halite pseudomorphs (Mayall, 1981). It contains very few fossils; microplankton are present but rare, and the only ichnotaxon identified is the U-shaped burrow *Arenicolites* (Mayall, 1981). It is considered to have been deposited in an evaporitic lacustrine environment. The Williton Member is very different. Its base is marked by an erosion surface, with *Diplocraterion* burrows, and the rest of the unit consists of grey shales interbedded with fine sands and silts. Shell beds are common, and the Member is well bioturbated, with ichnotaxa such as *Rhizocorallium, Planolites* and *Muensteria* (Mayall, 1981). It is considered to have been deposited in a fully marine environment (Mayall, 1981).

The Westbury Formation, the basal division of the Penarth Group, disconformably overlies the Blue Anchor Formation. It comprises mainly dark grey shales, occasionally interbedded with thin limestones and sandstones (Tuweni and Tyson, 1994). At its base there is often a distinctive but discontinuous conglomeratic unit containing abundant vertebrate material. This 'basal bone bed' is particularly well developed in the Bristol region, such as at Aust Cliff. There are several other units of fossil-rich sands within the formation, but the basal bone bed commonly differs from these in its larger average clast size (Trueman *et al.* 2003). The depositional environment of the Westbury Formation was broadly marine, with deposition occurring in relatively low energy conditions in shallow waters. The presence of the bone beds has been taken to indicate periodic storm activity (Tuweni and Tyson, 1994).

3. Materials and Methods

Of the fossil material used in this study, two samples were collected by Mike Curtis from a borehole core recovered by Geotechnical Engineering Ltd at Stoke Gifford in 2008 (Fig. 1). One sample (named Br.co.08-5 by Curtis) came from the Blue Anchor Formation, the other (Br.co.08-3) from the Westbury Formation (Fig. 2A). Both samples were processed

and sorted by Curtis. According to his notes, the samples were soaked in water and the resulting sediment was washed through 2.4 mm, 1.2 mm, 600 μm and 300 μm sieves, according to methods outlined by Korneisel *et al*. (2015).

A critical question concerns the origin of the lower sample. Was it really from the Blue Anchor Formation? The lithological log of the Stoke Gifford borehole (Fig. 2A) confirms the levels of the bone beds. Mike Curtis identified the Blue Anchor/Westbury contact at a depth of 10.5 m in the borehole, marked by the usual switch from grey-green mudstone below to the overlying finely bedded black shales and thin bone beds, each 20–30 mm thick, over a range of 220 mm in all. The lower bone bed, his Br.co.08-5, occurred 0.5–0.7 m below the base of the Westbury Formation (depth in borehole, 11.0-11.2 m). Curtis measured 0.5 m of grey-green mudstone below the Westbury basal bone bed and, below that, a further 0.5 m of grey mudstone from a depth of 11.0-11.5 m. This grey mudstone was rubbly towards the base and contained grey-green Blue Anchor Formation intraclasts and grey mudstone clasts up to 20 mm across. Curtis processed a sample from the top 200 mm of this grey mudstone. He noted also that the same succession, and the same Blue Anchor Formation bone bed, were noted in a second borehole 80 m away from the first borehole.

Four additional samples were collected by two of the authors (E. Landon and C. Hildebrandt) nearby, from an exposure of the Westbury Formation near Bristol Parkway railway station (Figs. 1, 2B, 3). Of these, only samples 2 and 3 yielded any fossil material, and only sample 3 yielded them in significant quantities. The samples were soaked in buffered 5% acetic acid (1.9 l of water in which 3 g of tri-calcium and 5 g of sodium carbonate anhydrous had been dissolved, and at least 100 ml of acetic acid was added) for 48 hours, and then washed through 2 mm, 850 m, 600 μm and 212 μm sieves. They were then soaked in water for 48 hours, with a small amount of soap to neutralise the acid, and the sediment washed through the sieves again. This cycle was repeated five times.

4. Systematic Palaeontology

4.1. Chondrichthyes

4.1.1. Duffinselache holwellensis *(Duffin, 1998b)*

These teeth are found in Br.co.08-3 and Br.co.08-5. All specimens (Fig. 4A–C) are incomplete, generally missing either the mesial end or the distal end, but show most of the root and the central cusp. The teeth are elongate, with a low crown ornamented with coarse non-branching ridges that ascend from the crown/root junction to the crown shoulder both labially and lingually. Distally, the ridges attain the occlusal crest, a longitudinal ridge that passes from end to end of the crown surface in the midline. The central cusp is smooth and asymmetric, inclined towards the distal end of the tooth. The root is rectangular with a flat basal surface and vascular foramina extending longitudinally both labially and lingually.

4.1.2. Hybodus cloacinus *(Quenstedt, 1858)*

Only one tooth was found, in Br.co.08-3. The specimen (Fig. 4D–E) is incomplete, missing the root, central cusp and mesial end. The two cusplets preserved are high and pointed, ornamented with vertical ridges that ascend almost to the apex, and bifurcate basally.

4.1.3. Lissodus minimus *(Agassiz, 1839)*

Lissodus was found only in Br.co.08-5, represented by 16 specimens, all of them incomplete (Fig. 4F–G). They generally lack the root and both the mesial and distal ends. The central cusp is low, smooth, and bulbous, with a more pronounced bulge labially. Lateral cusplets are absent, due to the incompleteness of the specimens. The crown bears a longitudinal ridge, the occlusal crest, which extends mesiodistally along the length of the crown, bisecting it.

4.1.4. Rhomphaiodon minor *(Agassiz, 1837)*

These teeth were found only in Br.co.08-5. They (Fig. 4H–I) are multicuspid, with one large central cusp, flanked by a pair of lateral cusplets. Both cusp and cusplets are high and pointed, with coarse ridges that descend from the cusp apices. They are lingually inclined. The root is shallow and wide, with a lingually offset, concave base.

4.1.5 Other selachian remains

More than 300 denticles were recovered from the three fossiliferous samples. Most were found in Parkway 3, and much of the remainder in Br.co.08-3. Isolated denticles cannot be assigned to any particular taxon because of the well-known ontogenetic changes and morphological variation across the body in sharks (Duffin, 1999). Consequently, we describe the denticles according to their shape and form.

Placoid denticles, typical of neoselachian sharks and pre-Rhaetian hybodonts, are the most common type of denticle present, and have been sorted by morphology into four types, termed Types 1–4.

Type 1 (Fig. 5A–B): Basal plates are rhomboid and attached to the crown by a small ridged pedicle. The crown is posteriorly directed and has three ridges extending from the anterior edge to the crown tip. The largest ridge extends down the centre of the crown, flanked by two smaller ridges on the edges of the crown. Present in Br.co.08-3 and Parkway 3.

Type 2 (Fig. 5C–D): Basal plates vary between rhomboid and ellipsoid, and are attached to the crown by a small pedicle, smooth in some specimens, ridged in others. The crown is posteriorly directed and rounded, with a smooth surface. The dorsal surface of the crown is ornamented with fine ridges at the anterior margin where it attaches to the pedicle.

These denticles closely resemble those recorded from Lower Jurassic synechodontiform sharks (Duffin and Ward 1993, fig. 12e). Present in Br.co.08-5, Br.co.08-3 and Parkway 3.

Type 3 (Fig. 5E–F): Basal plates are rhomboid and attached to the crown by a short pedicle, which varies in surface smoothness between specimens, as in type 2. The crown is posteriorly directed and similar in morphology to type 2, but with a central ridge that is wider and flatter. As with type 2, the dorsal surface has ornamentation at the anterior margin where the crown meets the pedicle. Present in Br.co.08-3 and Parkway 3.

Type 4 (Fig. 5G): These denticles lack a basal plate. The pedicle is cylindrical and strongly ridged. The crown is ellipsoid, low and generally flat, occasionally slightly domed. The crown surface is smooth and unornamented. Present in Br.co.08-5, Br.co.08-3 and Parkway 3.

Dermal denticle A (Fig. 5H–J): Only one specimen was found, in Parkway 3. The basal plate has coarse ridges extending from the base of the hook out to the edges of the plate, and narrows to a smooth hook that is ellipsoid in section. It resembles the specialised scales found on the underside of the frontal clasper and the opposing surface of the snout in Jurassic squalorajoid holocephalians (Delsate et al, 2002, fig. 21).

Dermal denticle B (Fig. 5K–L): Only one specimen was recovered, in Parkway 3. The basal plate is asymmetric and ridged, extending into a conical crown. The base has a large foramen that extends into the tissues of the crown.

Dermal denticle C (Fig. 5M): There are two specimens, both from Br.co.08-3. The basal plate is not preserved. The crown is low, with a smooth surface, and the apex comes to a slight point. Denticles of this morphotype have previously been recorded from the Westbury Formation of Chilcompton (Duffin 1999, pl. 27 fig. 3).

Hybodont scales (Fig. 5N–O): There are two specimens, one from Br.co.08-3 and one from Br.co.08-5. The scale lacks a basal plate. The pedicle is cylindrical, with coarse vertical

ridges. The crown has a quadrate outline in dorsal view and is ornamented with fine posterior-anterior ridges on the dorsal surface and coarse ridges at the sides that do not extend onto the dorsal surface.

Ctenacanthid scales (Fig. 5P–Q): Two examples were found, one in sample Br.co.08-3 and one in Br.co.08-5. The basal plate is rectangular, with a multicuspid crown. The cusps are recurved and laterally fused, with pronounced ridges that extend from the apex to the base.

Chimaeriform scales (Fig. 5R): Only one example was found, in sample Br.co.08-5. The basal plate is large and oval, with coarse ridges that extend from base to crown. The crown is low and slightly domed, with a smooth surface.

Neoselachian vertebrae (Fig. 5S-T): These centra are cylindrical and short, with subcircular, concave articular faces.

4.2. Actinopterygii

4.2.1. Gyrolepis albertii *(Agassiz, 1835)*

These teeth (Fig. 6A) are present in all three samples and are the most common actinopterygian teeth present. They are conical, with a curved root that flares slightly at the base. The apical cap is enamelled and translucent and comes to a sharp point. It makes up approximately 30% of total tooth height. The specimens collected vary in size and degree of wear.

4.2.2 Severnichthys acuminatus *(Agassiz, 1835)*

There are two distinct types of teeth associated with this species, each originally assigned to a separate genus (Duffin, 1999). However jaw fragments have been found that

include both types of teeth, as well as a range of morphologies between the two end-members. Consequently, they were combined into a single taxon by Storrs (1994).

Birgeria acuminata-type (Fig. 6B–C): These are present in Br.co.08-3 and Br.co.08-5. The teeth are conical and sharply pointed. The crown is slightly compressed to form lateral cutting edges (Fig. 6C). The apex of the crown is translucent, and the crown is ornamented with prominent vertical ridges ascending to the apex. The crown is separated from the root by a fairly prominent ridge. The root is ornamented with fine vertical ridges.

Saurichthys longidens-type (Fig. 6D–E): These are present in Br.co.08-3 and Br.co.08-5. The teeth are conical and slightly sigmoidal in shape, with a smooth translucent cap that is much smaller than that of *B. acuminata* type. Below the cap the tooth is coarsely ridged.

4.2.3. Sargodon tomicus *(Plieninger, 1847)*

Only three *S. tomicus* teeth were found, two in Br.co.08-5 and one possible specimen from Br.co.08-3. All the specimens (Fig. 6F) are molariform, with smooth, domed crowns that are ellipsoid in occlusal view. The roots are not preserved.

4.2.4. Unidentified teeth

Three of the tooth morphotypes found in the samples could not be identified. Tooth B and tooth C have previously been identified as shark gill raker teeth and assigned by Duffin (1998a) to *Pseudocetorhinus pickfordi* by association. These morphotypes were figured by Duffin (1998a, 1999, pl. 27 fig. 2) and Mears et al. (2016, fig. 5n). We consider this association to be erroneous, however, and regard these teeth as osteichthyan.

Tooth A (Fig. 6G): present in Parkway 3 only. The tooth is smooth and straight, with a smooth rounded cap that constitutes approximately 10% of total tooth height.

Tooth B (Fig. 6H): present in Parkway 3 only. The tooth is smooth, with a long curving shaft and a pointed translucent cap that constitutes approximately 10% of total tooth height.

Tooth C (Fig. 6I): present in Br.co.08-3 and Parkway 3. The shaft is straight, with a smooth pointed cap that curves slightly. The cap constitutes approximately 30% of total tooth height.

4.2.5. Other actinopterygian remains

Osteichthyan scales are common in all three samples, although in most cases they are extremely fragmented. The whole specimens have been divided by morphotype.

Morphotype 1 (Fig. 6J): Rhombohedral, with a slight ridge on the ventral surface that ends in a slight protuberance. The dorsal surface is worn, but retains some enamel, which is ridged diagonally. This is similar to the morphotype S2 osteichthyan scale illustrated by Mears et al. (2016, fig. 10c, d) from Hampstead Farm Quarry, Chipping Sodbury.

Morphotype 2 (Fig. 6K): Same shape and enamel patterning as in morphotype 1, but lacking the protuberance.

Morphotype 3 (Fig. 6L): The shape of these scales is less rhomboid, and closer to square. The enamel is diagonally ridged, as in morphotypes 1 and 2, but in most specimens the enamel has been completely worn away to leave a series of concentric rings on the dorsal surface. This is similar to the internal view of a morphotype S4 osteichthyan scale illustrated by Mears et al. (2016, fig. 10g, h) from Hampstead Farm Quarry, Chipping Sodbury.

Morphotype 4 (Fig. 6M): These scales are ellipsoid in shape. The enamel morphology is the same as in the previous three morphotypes and similar to scales widely identified as belonging to *Gyrolepis albertii* (e.g. Mears et al., 2016, fig. 10a, b).

Fin ray elements: These are extremely common in all three samples, with more than 200 specimens.

4.3. Invertebrates

4.3.1. Echinodermata

Echinoderm remains were found only in samples Br.co.08-3 (Westbury Formation) and Br.co.08-5 (Blue Anchor Formation). They are abundant in the Blue Anchor Formation sample, which is dominated by disarticulated remains of small echinoids and ophiuroids. The sample from the Westbury Formation yielded just two echinoid spines and no other echinoderm remains. Spines (Fig. 7A) and fragmentary ambulacral (Fig. 7B) and interambulacral (Fig. 7C) plates can be assigned to the echinoid genus *Diademopsis*, while numerous lantern elements (hemipyramids, rotulas, epiphyses, teeth) probably also can be assigned to this genus. *Diademopsis serialis* (Agassiz, 1838) is common in the basal Lias Group across much of the UK (Smith, 2015) and is also known from the upper Penarth Group (Smith, 1990), but the material we have described here is too poorly preserved to establish that it is the same species. Ophiuroid vertebrae (Fig. 7D, E) and arm shields (Fig. 7F, G) are similarly abundant but lack clear diagnostic features. Many of the lateral arm shields resemble those of *Palaeocoma*, a genus represented by several Early Jurassic species (Hess, 1960, 1962). Some of the vertebrae are more reminiscent of the genus *Aplocoma*, which is represented at several Penarth Group sites across the UK by *Aplocoma damesi* (Wright, 1874) (Hess, 1965, but see also Thuy et al., 2012).

Together with the abundant echinoid and ophiuroid material there are a small number of crinoid ossicles. Two small columnals recovered from the Blue Anchor Formation of Br.co.08-5 can be assigned to the genus *Isocrinus* (Fig. 7H-K) and among a few small brachial plates from the same sample, most probably also belong to this genus (Fig. 7L-M).

However, one small brachial (Fig. 7N-O) has a very large aboral ligament fossa with significantly smaller muscular fossae. Based on these characters, it is assigned tentatively to the genus *Pentacrinites* (Simms, 1989). Species of both *Isocrinus* and *Pentacrinites* are known from the Late Triassic of continental Europe and from the Early Jurassic of the UK (Simms, 1990a). Dissociated pentacrinitid ossicles, described as *Pentacrinites versistellatus* (Schafhäutl, 1851), are present in the Zlambach and Kössen formations, both Rhaetian in age, of Austria and Germany, with *Pentacrinites* represented in the Hettangian by numerous examples of *P. doreckae* (Simms, 1989). Simms (1989) considered that just one isocrinid species, *Isocrinus psilonoti* (Quenstedt, 1858), was present in the British Hettangian, but it is now evident that a separate species, *Isocrinus angulatus* (Oppel, 1856), occurs in the early Hettangian (Planorbis Zone) before the appearance of *I. psilonoti*. This small species has consistently angular columnal interradii whereas the columnals figured here are more rounded. It seems unlikely that they could be *I. psilonoti* since they significantly predate the first definite appearance of this species in the Hettangian, in the Liasicus Zone. Another species with rounded interradii, and of broadly similar age to the material figured here, is *Isocrinus bavaricus* (Winkler, 1861), from the Kössen Formation of Austria and Germany. However, neither the isocrinid nor pentacrinitid material we have described here is sufficiently diagnostic to be assigned to a particular species.

Ophiuroids are known to be relatively stenohaline compared with most other echinoderms, while the presence of abundant *Diademopsis* in the Penarth Group and basal Lias at many sites where typically stenohaline taxa (ammonites, brachiopods, crinoids) are absent suggests that this genus too may be relatively tolerant of salinity variations. However, isocrinid crinoids would appear to be much more strictly stenohaline judging from their distribution within the Lias Group, and so their occurrence within the Blue Anchor Formation is unexpected.

4.3.2. Mollusca

Bivalves are present in all three samples. In Parkway 3, they are preserved only as fragments of external moulds – it is likely that the original fossil material was destroyed during the acid digestion process. In both Br.co.08-3 and Br.co.08-5, there are some complete moulds as well as many shell fragments. The fragments suggest that most of the bivalves present in the assemblage had strongly ribbed shells.

Six specimens of cephalopods were identified, and they are present only in sample Br.co.08-3, in the form of arm hooks (Fig. 8A–B). They are black and appear to have been flattened post-mortem. All specimens lack spurs and appear to lack a base. They may have originally been hollow. In some specimens the uncinus is well differentiated and comes to a sharp point (Fig. 8A), whereas in others the uncinus is smaller and the apex worn and rounded (Fig. 8B). Unusually for cephalopod arm hooks, the inner margins of the specimens are distinctly sigmoidal (some more so than others), whereas the outer margin is arcuate in some (Fig. 8A) and slightly sigmoidal in others (Fig. 8B). All specimens lack a distinct orbicular scar.

There is only one gastropod in the collection, from Br.co.08-5. The specimen is preserved as an internal mould. It is planispiral and missing the apex.

4.4 Other fossilised remains

4.4.1. Coprolites

Samples Br.co.08-3 and Br.co.08-5 contain coprolites. These are generally light brown and of varying shape, some rounded, some flattened.

5. Discussion

5.1. Blue Anchor Formation: bone beds and crinoids

Bone beds have seldom been reported from the Blue Anchor Formation of south-west Britain. They might simply be rare, or have been overlooked, particularly if they occur close to the top of the unit where they might be conflated with the basal bone bed of the overlying Westbury Formation. However, bone beds and isolated vertebrate remains have been noted from the Blue Anchor Formation previously. Boyd-Dawkins (1864a, b) noted a fossiliferous unit containing bivalves and vertebrate remains in the foreshore section at Blue Anchor Point, in Somerset. Warrington and Whitaker (1984) designated this cliff the type section for the Blue Anchor Formation and stated Boyd-Dawkins' fossiliferous unit to be about 3.04 m below the Westbury Formation basal bone bed. As summarised by Warrington and Whitaker (1984), this horizon produced remains of the osteichthyans *Sargodon tomicus* and '*Saurichthys' apicalis*, as well as *Acrodus minimus*, *Gyrolepis alberti*, and *G. tenuistriatus* from this level, and from the top 1.83 m of the succession. Richardson (1905) reported discontinuous fossiliferous sands approximately 5 ft below the top of the Blue Anchor Formation at Goldcliff, which produced remains of *Gyrolepis albertii* and *Hybodus minor*.

Fish remains were also noted elsewhere in the upper part of the Blue Anchor Formation, including unidentified fish remains from c. 4.27 m below the top of the formation in the same area (Richardson, 1911, p. 18). At St. Audrie's Bay, Whittaker and Green (1983, p. 50) reported *Gyrolepis* and *Hybodus* cf. *cloacinus*, associated with teeth of *Sargodon* and '*Sphaerodus*' type 3.26 to 3.72 m below the top of the formation, and fish scales were noted within the top 1.52 m of the succession (Bristow and Etheridge, 1873; Whittaker and Green, 1983, p. 51). At Lilstock, Richardson (1911, p. 30) noted fish scales 2.41 m below the top of the formation. Plant (1856) and Harrison (1876) both report fish remains from outcrops of the Blue Anchor Formation in Leicestershire. Plant (1856) reported only scales, but Harrison

(1876) reported teeth tentatively assigned to the genus *Strophodus*, along with a selection of *Ichthyodorulites* (unassigned fin spine) specimens and some bone fragments.

Reptile remains from the uppermost part of the Blue Anchor Formation include rolled fragments of bone, recorded from 2.44 to 4.27 m below the top of the formation near Blue Anchor (Boyd-Dawkins 1864a, p. 398) and, most famously a supposed mammalian tooth, named *Hypsiprymnopsis rhaeticus*, from 3.20 m below the top of the formation near Blue Anchor (c. ST045438) (Boyd-Dawkins 1864a, pp. 409-412). This specimen is now lost, but it has since been reclassified simply as 'tritylodontid *incertae sedis*' (Clemens *et al*., 1979, p. 13).

These isolated reports have often been overlooked when the emphasis has been on the Rhaetian bone beds proper. Some confusion might have arisen because certain teeth, scales, and bones had been reported from the topmost bed ('bed 1') of the Sully Beds, which at one time was regarded as part of the Blue Anchor Formation (Richardson, 1911) but is now considered equivalent to the lower part of the overlying Westbury Formation (Warrington and Whitaker, 1984). Nonetheless, the examples noted here, from Warrington and Whitaker (1984), are all from the Blue Anchor Formation as currently defined.

It is perhaps no surprise to find such bone beds below the sharp disconformity that marks the beginning of the Rhaetian transgression proper. The Blue Anchor Formation documents a transition from the evaporitic lacustrine deposits of the lower Rydon Member to the fully marine, shallow water deposits of the overlying Williton Member (Mayall, 1981). The succession records numerous minor transgressions and regressions that become more distinctly marine towards the top. Palynomorphs confirm the sedimentary evidence (Warrington and Whitaker, 1984), demonstrating a change from an essentially terrestrial environment, represented by the underlying red beds of the Mercia Mudstone Group and the lower part of the Blue Anchor Formation, to one increasingly influenced by transgressive

marine conditions in the upper units of the Blue Anchor Formation and overlying Penarth Group.

Echinoid and ophiuroid ossicles are not uncommon at certain levels in the Penarth Group (e.g. Mears et al. 2016, fig. 17h–u) and particularly in the succeeding Lias Group. Our discovery of echinoid and ophiuroid remains in the underlying Blue Anchor Formation at this site is the first record of such taxa in the British Triassic below the Penarth Group and provides evidence of substantially marine salinity in this part of the Triassic succession. The echinoid and ophiuroid taxa present are considered to have been marginally euryhaline, but the unexpected presence alongside them of a few isocrinid crinoid ossicles suggests that the local environment at this time was at or very close to fully marine salinity. Until now the earliest Mesozoic crinoids reported in the UK were from the basal Lias Group, less than 4 m below the first appearance of *Psiloceras planorbis* in the Larne section in Northern Ireland (Simms and Jeram 2007). Crinoids are unknown from the British Penarth Group and so these few ossicles (two columnals and a few brachials) represent the first discovery of Triassic crinoids in Britain. Reworked Carboniferous fossils are not uncommon in bone-bearing horizons within coeval fissure and cave deposits (Duffin, 1999, Simms, 1990b), and have been reported from the basal bone bed at Aust (Macfadyen, 1970), but the echinoderm material described here is of specifically Mesozoic aspect and is presumed to be contemporary with all the other associated fossils. It is certainly not derived Carboniferous material.

5.2. Fish

The three samples together yielded approximately 3000 fish specimens, including broken and unidentifiable fragments. The bulk of this material came from Br.co.08-3, with approximately 1600 specimens, then from Br.co.08-5, with approximately 900 specimens,

and Parkway 3, with 455 specimens. Br.co.08-5 yielded the most chondrichthyan material, with 57% of identifiable teeth being chondrichthyan. In the younger Br.co.08-3, however, only 8% of identifiable teeth were chondrichthyan, and chondrichthyan teeth were not present in Parkway 3 at all.

Br.co.08-3 contains only two identifiable chondrichthyan taxa – *Hybodus cloacinus* and *Duffinselache holwellensis*, with *D. holwellensis* making up 93% of the population. In Br.co.08-5, however, the chondrichthyan population is dominated by the species *Lissodus minimus* (67% of the population). A mere 8% of the identifiable chondrichthyan teeth from this sample were *D. holwellensis*, and *H. cloacinus* was not present at all, the remaining 25% of identifiable teeth being *Rhomphaiodon minor*.

The osteichthyans, conversely, show a more constant pattern across all three samples – all are dominated by a single taxon, *Gyrolepis albertii*. This fish is most abundant in the two Westbury Formation samples, making up 88% of the osteichthyan population in Br.co.08-3, 86% in Parkway 3, and 61% in Br.co.08-5.

A Simpson's Diversity Index yields values of 0.33 and 0.3 for Br.co.08-3 and Parkway 3, respectively, and 0.77 for Br.co.08-5, confirming that the last sample has a much higher biodiversity. This also suggests that a higher diversity of organisms was present in the seas that deposited the Blue Anchor Formation than those of the upper Westbury Formation, but this may be a bias in the data – neither Br.co.08-3 nor Parkway 3 samples the basal Westbury Formation bone bed, which has proven the richest in previous studies (e.g. Swift and Martill, 1999; Allard et al., 2015).

One very clear faunal change between the Blue Anchor and the Westbury formations is seen in the proportions of osteichthyans to chondrichthyans. In the Blue Anchor Formation, the two groups are nearly equally abundant, with 57% of identifiable teeth being osteichthyan and 43% of identifiable teeth being chondrichthyan. In the Westbury Formation, Br.co.08-3 is

very much dominated by osteichthyans, which make up 92% of the identifiable teeth, and chondrichthyan teeth are not present in Parkway 3 at all, although the sample contained plenty of chondrichthyan denticles.

5.3. Cephalopods

The most unexpected find was the six cephalopod hooklets in the Br.co.08-3 sample (Fig. 8). These were initially identified as scolecodonts (polychaete jaw elements), but scolecodonts typically have a more complex morphology, such as a serrated inner margin, and they tend to be dark brown (Kulicki and Szaniawski, 1972). The specimens from Br.co.08-3 are much simpler in form, and a dull black. They most closely resemble grasping hooklets from the arms of coleoid cephalopods. These hooklets are often misinterpreted as scolecodonts on account of their similar morphology and, to add further confusion, isolated cephalopod hooklets are frequently found in association with scolecodonts (Kulicki and Szaniawski, 1972).

The Coleoidea is a monophyletic group of cephalopods that includes cuttlefish, squids and octopuses, characterised by their lack of an external shell. The Coleoidea are divided into two clades, Octobrachia and Decabrachia, that are widely accepted as monophyletic taxa (Doyle et al., 1994; Donovan and Fuchs, 2012; Fuchs et al., 2015) based on their eight and ten arms respectively, and other characters. Octobrachians date from the Triassic to the present day, and decabrachians from the Late Cretaceous to the present day. Further clades include the Phragmoteuthida from the Triassic and Jurassic, sister clade to the Octobrachia; the Belemnitidae from the Triassic to Cretaceous; the Diplobelida from the Jurassic and Cretaceous, both outgroups of the Decabrachia; and the Aulaceratida from the Permian to Jurassic, a basal clade of coleoids.

Coleoid cephalopods first appeared in the Carboniferous and diversified through the Permian and Triassic, when belemnitids, phragmoteuthids, and octobrachians all appeared. There was a further radiation in the Jurassic together with the diplobelids. Consequently there are five possible coleoid clades in the Late Triassic and Early Jurassic to consider as possible sources of the cephalopod hooklets from Stoke Gifford: Aulaceratida, Belemnitida, Diplobelida, Phragmoteuthida, and Octobrachia.

Several families of Recent and extinct coleoids possess hooks on their arms, and in some groups, on their tentacles as well. In Recent coleoids, arm hooks are known from the families Onychoteuthidae, Enoploteuthidae, Octopoteuthidae, Gonatidae and Cranchiidae of the order Teuthida (Engeser and Clarke, 1988). Pre-Cenozoic arm hooks are known only from the now extinct belemnoid coleoids (Engeser and Clarke, 1988) and phragmoteuthid coleoids (Doyle *et al.* 1994).

Fossilised arm hooks are most commonly found loose in marine sediments, but have also been found in association with belemnoid and phragmoteuthid shells (Engeser and Clarke, 1988), sometimes in life position in exceptionally preserved individuals. They can also be found in the stomach contents, regurgitates and, less frequently, in coprolites of marine predators such as ichthyosaurs and plesiosaurs (Pollard, 1968; Doyle and Macdonald, 1993; Wahl, 1998).

The arm hooks of Recent cephalopods are chitinous, and it is thought that those of early cephalopods were also chitinous (Engeser and Clarke, 1988). The fossil hooks are frequently found fractured or broken, and are usually dull black (Fig. 8; Engeser and Clarke, 1988). The three principal morphological features of fossil arm hooks are the base, the shaft and the uncinus (Fig. 9A). Variations on this form include internal and external spurs (Fig. 9B–C), extended hook bases, and the curvature of the uncini (Kulicki and Szaniawski, 1972; Engeser and Clarke, 1988). Particular features of interest when comparing fossil forms to

Recent ones are the orbicular scar (the margin up to which the hook was covered in soft tissue), the spur, and the base, which would have been enclosed in muscle and would have attached the hook to the arm. The latter is important because it makes it clear that the arm hooks of fossil coleoids were not derived from a sucker ring, as in modern coleoids (Engeser and Clarke, 1988).

Isolated cephalopod arm hooklets are difficult to assign to specific coleoid taxa, as the shape and size of hooklets can vary along the length of the arm. Identification of the specimens from Br.co.08-3 is made more difficult as they do not seem to match the shape of any other belemnoid arm hooks, and in all specimens the base appears to be broken off. The typical belemnoid arm hook tends to be slender, with an arcuate outer margin and an inner margin that is either arcuate or straight and, as mentioned previously, may have spurs. The hooklet specimens from Br.co.08-3 have slightly varied shapes, but they all have a sigmoidal inner margin, and the outer margin is arcuate in some, and gently sigmoidal in others.

Whilst not fitting any of the basic belemnoid hook shapes shown by Engeser and Clarke (1988), the Br.co.08-3 specimens resemble the hooklets of the Carboniferous coleoid *Jeletzkya douglassae* (Johnson and Richardson, 1968, fig. 1), especially the hook shown in Figure 8A. The hooklets also bear a resemblance to the arm hooks of the late Triassic *Phragmoteuthis bisinuata* (Doguzhaeva et al., 2007, fig. 2C; Fuchs et al., 2013, fig. 4E), allowing for some post-mortem flattening. The second hook (Fig. 8B) resembles those figured by by Trammer (1978; pl. 1, figs. 5, 6 and pl. 2 figs. 1–5), which were assigned to the phragmoteuthids, although not to any particular species. However, it also resembles belemnitid hooklets from the Jurassic and Cretaceous. If this is the correct assignment then it would be a most unexpected find in pre-Jurassic rocks (Robert Weis, pers. comm., 2015).

It is most likely that the hook specimens from Br.co.08-3 were from phragmoteuthid or belemnitid coleoids, rather than a diplobelid coleoid, based on their morphology. The

phragmoteuthids and belemnitids are also known to have been present in Late Triassic seas, whereas the diplobelids are known only from the Jurassic and Cretaceous.

6. Conclusions

The vertebrate faunas of samples Br.co.08-3 and Parkway 3 are typical of the Westbury Formation. The lack of chondrichthyan teeth in Parkway 3 is curious but may be no more than a sampling bias, as chondrichthyan denticles are abundant in the samples. Sample Br.co.08-3 is significant in yielding evidence, in the form of hooklets, for the first discovery of Rhaetian coleoid cephalopods in the UK. These hooklets probably can be assigned to members of the clades Phragmoteuthida or Belemnitida.

The diversity of echinoderm remains was also unexpected. Here we report the first crinoid remains from the British Triassic, and the most diverse assemblage of Rhaetian echinoderm remains from the British Rhaetian. The echinoderm remains in the Blue Anchor Formation samples confirm their high salinity at the time.

The vertebrate fauna from Br.co.08-5 is very similar to that of the lower part of the Westbury Formation, despite being from the older Blue Anchor Formation. Of particular significance among the associated invertebrate fauna are ossicles of isocrinid and pentacrinitid crinoids. These are the first crinoid remains to be discovered in the British Triassic and indicate a brief period of near stenohaline conditions.

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the crinoid remains. We thank Steve Donovan and an anonymopus reviewer for their comments on the MS.

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Fig. 1. Geological map of the Stoke Gifford area, with flags indicating the three sample sites.

Fig. 2. Sedimentary logs, of Stoke Gifford borehole BH05 (A) and the Parkway site (B). Log A was compiled from data collected by Geotechnical Engineering Ltd during the drilling process, and notes from Mike Curtis. Log B is based on fieldwork in 2015.

Fig. 3. Photograph of the exposure, thinly covered by fresh grass, sampled near Bristol Parkway railway station. (A) Overview of the sample site and its position relative to the station car park. (B) Closer view of the exposure, hammer for scale. Sample 1 was taken 1 m above sample 3 (exposure concealed by line of bushes), sample 3 was taken just above the line of bushes, and sample 2 taken halfway between the line of bushes and the contact with the Blue Anchor Formation. Sample 4 was taken from the same level as sample 2, from a locality approximately 100 m away.

Fig. 4. Chondrichthyan teeth. (A-C) *Duffinselache holwellensis* (BRSUG 29371-2-171-11-2), in labial (A), lingual (B) and occlusal views (C). (D-E) *Hybodus cloacinus* (BRSUG 29371-2-171-12), labial (D) and occlusal views (E). (F-G) *Lissodus minimus* (BRSUG 29371-1-427-1), labial (F) and occlusal views (G). (H-I) *Rhomphaiodon minor* (BRSUG 29371-1-428-1), lingual (H) and labial views (I). All scale bars equal 0.5 mm.

Fig. 5. Chondrichthyan denticles and vertebrae. (A-B) Placoid denticle type 1 (BRSUG 29385-18-2), surface (A) and anterior views (B). (C-D) Placoid denticle type 2 (BRSUG 29385-19-2), surface (C) and anterior views (D). (E-F) Placoid denticle type 3 (BRSUG 29385-20-2), surface (E) and anterior views (F). (G) Placoid denticle type 4 (BRSUG 29371-2-171-28-2) lateral view. (H-J) Dermal denticle A (BRSUG 29385-22), anterior (H),

posterior (I) and surface views (J). (K-L) Dermal denticle B (BRSUG 29385-17). (M) Dermal denticle C (BRSUG 29371-2-171-32-2), surface view. (N-O) Hybodont denticle (BRSUG 29371-1-469-1), surface (N) and lateral views (O). (P-Q) Ctenacanthid scale (BRSUG 29371-1-470), surface (P) and anterior views (Q). (R) Chimaeriform denticle (BRSUG 29371-1-458), surface view. (S-T) Neoselachian vertebrae (BRSUG 29371-2-171-10-2), axial (S) and lateral views (T). All scale bars equal 0.5 mm.

Fig. 6. Osteichthyan teeth and scales. (A) *Gyrolepis albertii* (BRSUG 29371-2-171-13-2). (B-E) *Severnichthys acuminatus*; (B-C) *Birgeria acuminata*-type (BRSUG 29371-2-171-14-2), (D-E) *Saurichthys longidens*-type (BRSUG 29371-2-171-15). (F) *Sargodon tomicus* (BRSUG 29371-1-452), occlusal view. (G) Unidentified tooth A (BRSUG 29385-14). (H) Unidentified tooth B (BRSUG 29385-15). (I) Unidentified tooth C (BRSUG 29371-2-171-16-1). (J) Osteichthyan scale morphotype 1 (BRSUG 29371-2-171-21-2). (K) Osteichthyan scale morphotype 2 (BRSUG 29371-2-171-22-2). (L) Osteichthyan scale morphotype 3 (BRSUG 29371-2-171-23-2). (M) Osteichthyan scale morphotype 4 (BRSUG 29371-2-171-24-2). All scale bars equal 0.5 mm.

Fig. 7. Echinoderm remains from the bone bed near the top of the Blue Anchor Formation. (A-C) Echinoid fragments. (A) Primary spine of *Diademopsis* sp. (BRSUG-29371-1-440-1). (B) Ambulacral plate of *Diademopsis* sp. (BRSUG 29371-1-473-1). (C) Interambulacral plate of *Diademopsis* sp. (BRSUG 29371-1-439-1. (D-G) Ophiuroid ossicles. (D-E) Ophiuroid vertebra (BRSUG 29371-1-474-1). (F-G) Lateral arm shield of *Palaeocoma* sp., exterior (F) and interior (G) (BRSUG 29371-1-474-2). (H-O) Crinoid ossicles. (H-I) Interradial fragment of columnal of *Isocrinus* sp. (BRSUG 29371-1-454). (J-K) Proximal columnal of juvenile

Isocrinus sp. (BRSUG 29371-1-442). (L-M) Isocrinid brachial (BRSUG 29371-1-455). (N-O) Pentacrinitid brachial (BRSUG 29371-1-446). All scale bars equal 0.5 mm.

Fig. 8. Cephalopod hooklets, possibly phragmoteuthid or belemnitid. (A) BRSUG 29371-2-171-33-2. (B) BRSUG 29371-2-171-33-3. Scale bar equals 0.2 mm.

Fig 9. Schematic diagrams of a typical fossil cephalopod hooklet, showing the principal morphological features (A); a hooklet with an internal spur (B); and a hooklet with an external spur (C). Modified from Engeser and Clarke (1988).

Figure 1

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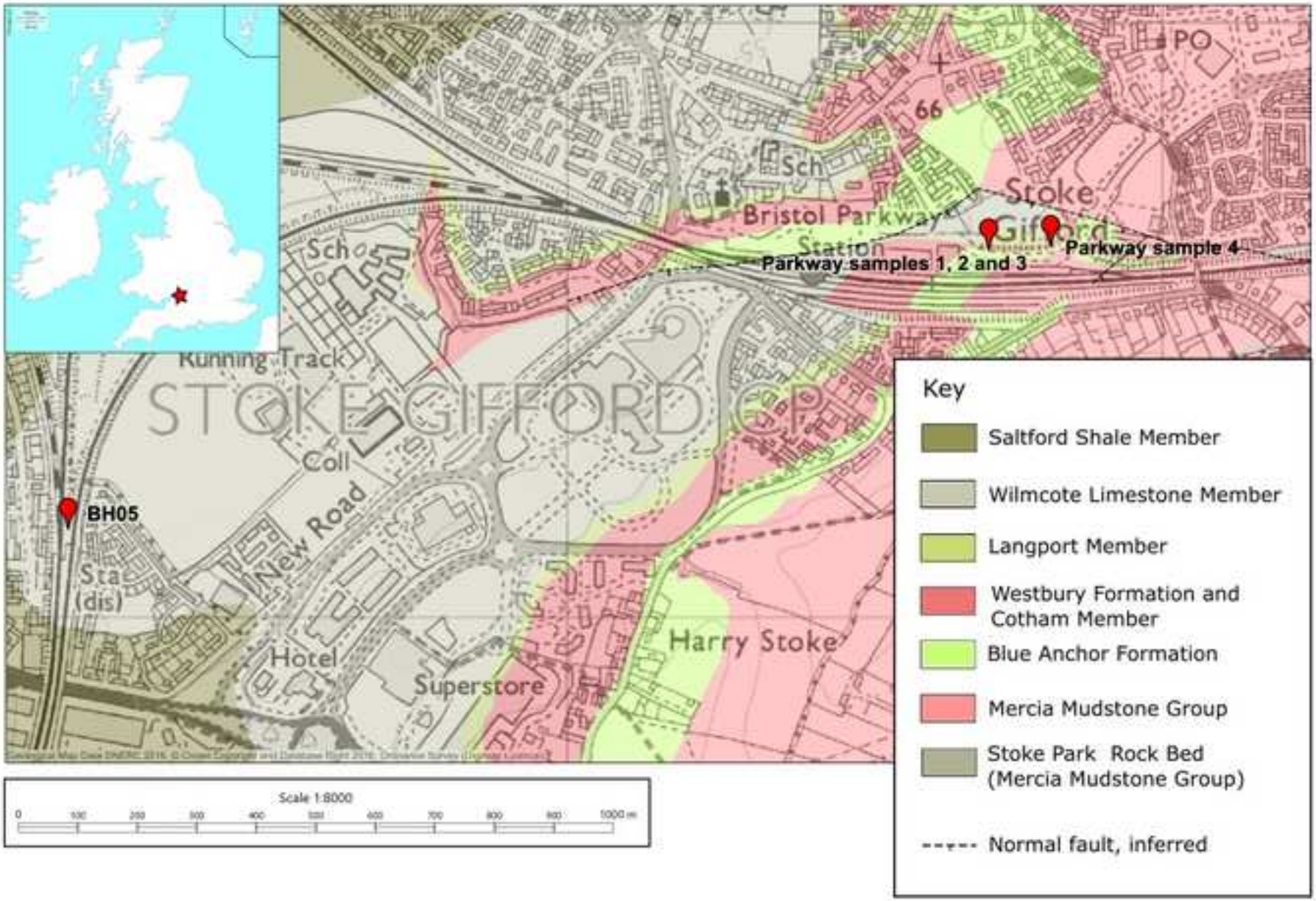

Figure 2

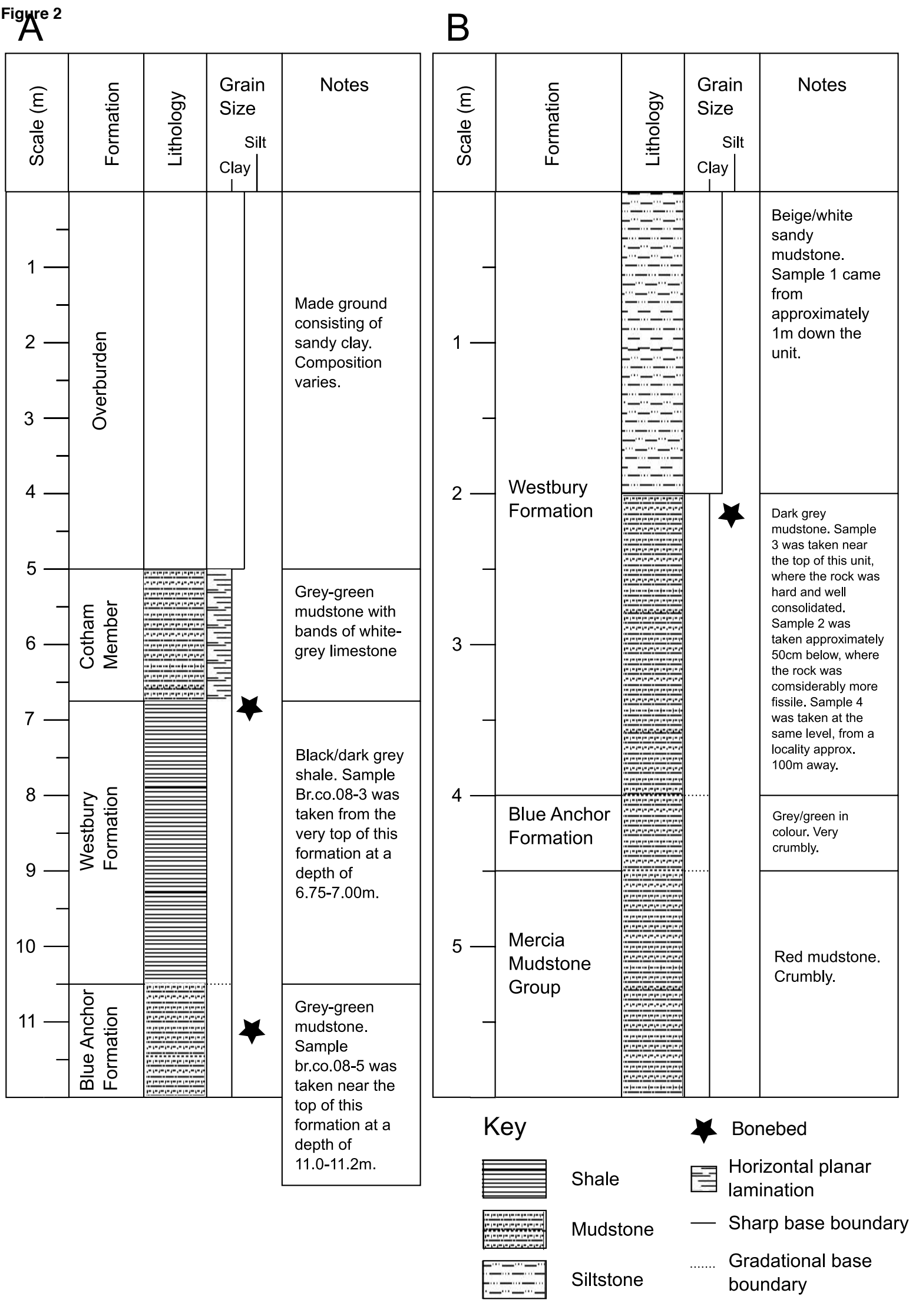
A
Scale (m)
Formation
Lithology
Grain Size
Silt
Clay
Notes
1
2
3
4
5
6
7
8
9
10
11
Overburden
Made ground consisting of sandy clay. Composition varies.
Cotham Member
Grey-green mudstone with bands of white-grey limestone
Westbury Formation
Black/dark grey shale. Sample Br.co.08-3 was taken from the very top of this formation at a depth of 6.75-7.00m.
Blue Anchor Formation
Grey-green mudstone. Sample br.co.08-5 was taken near the top of this formation at a depth of 11.0-11.2m.
B
Scale (m)
Formation
Lithology
Grain Size
Silt
Clay
Notes
1
2
3
4
5
Westbury Formation
Beige/white sandy mudstone. Sample 1 came from approximately 1m down the unit.
Dark grey mudstone. Sample 3 was taken near the top of this unit, where the rock was hard and well consolidated. Sample 2 was taken approximately 50cm below, where the rock was comsiderably more fissile. Sample 4 was taken at the same level, from a locality approx. 100m away.
Blue Anchor Formation
Grey/green in colour. Very crumbly.
Mercia Mudstone Group
Red mudstone. Crumbly.
Key
Shale
Mudstone
Siltstone
Bonebed
Horizontal planar lamination
Sharp base boundary
Gradational base boundary

Figure 3

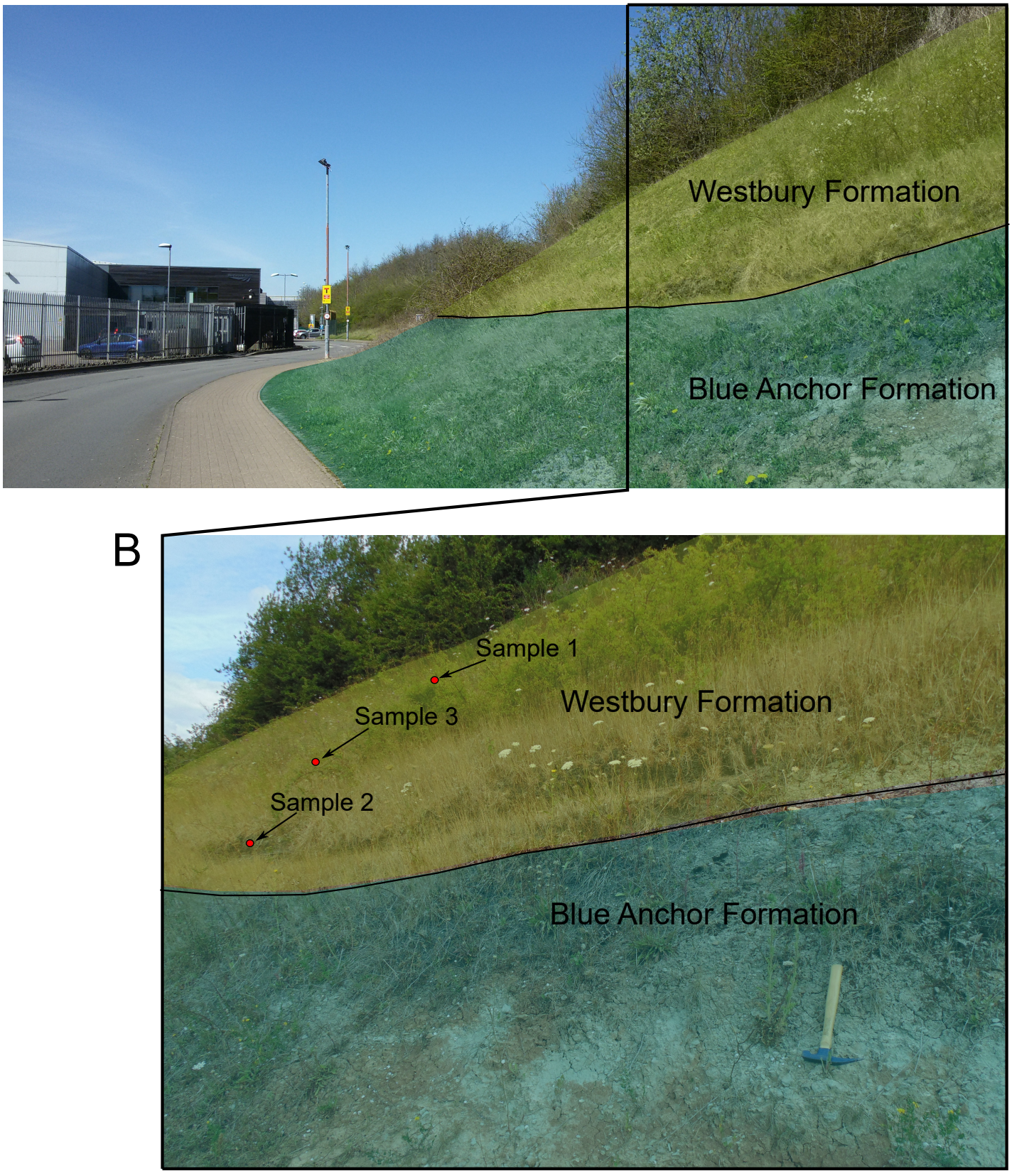
A
Westbury Formation
Blue Anchor Formation
B
Sample 1
Sample 3
Sample 2
Westbury Formation
Blue Anchor Formation

Figure 4

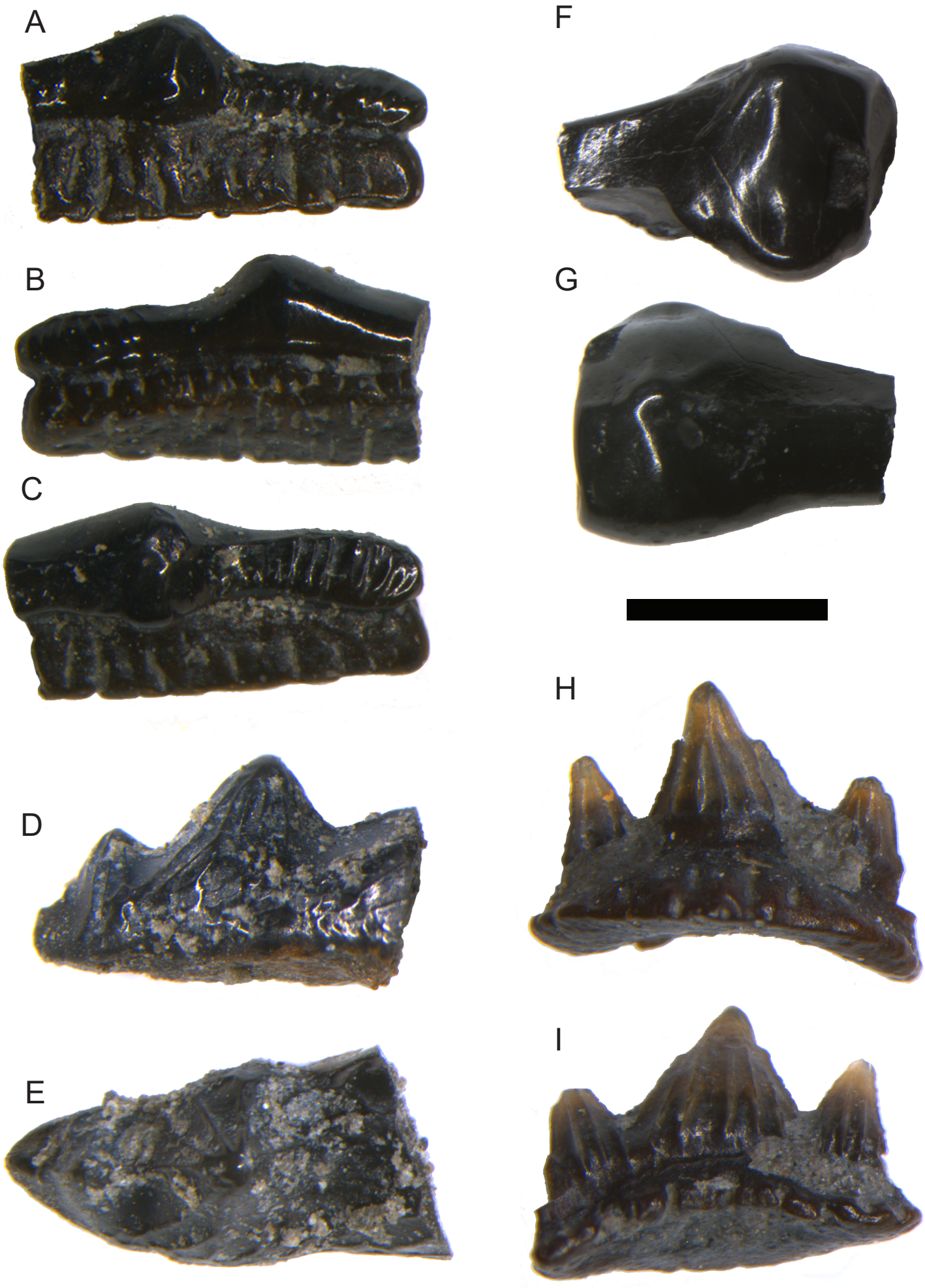

Figure 5

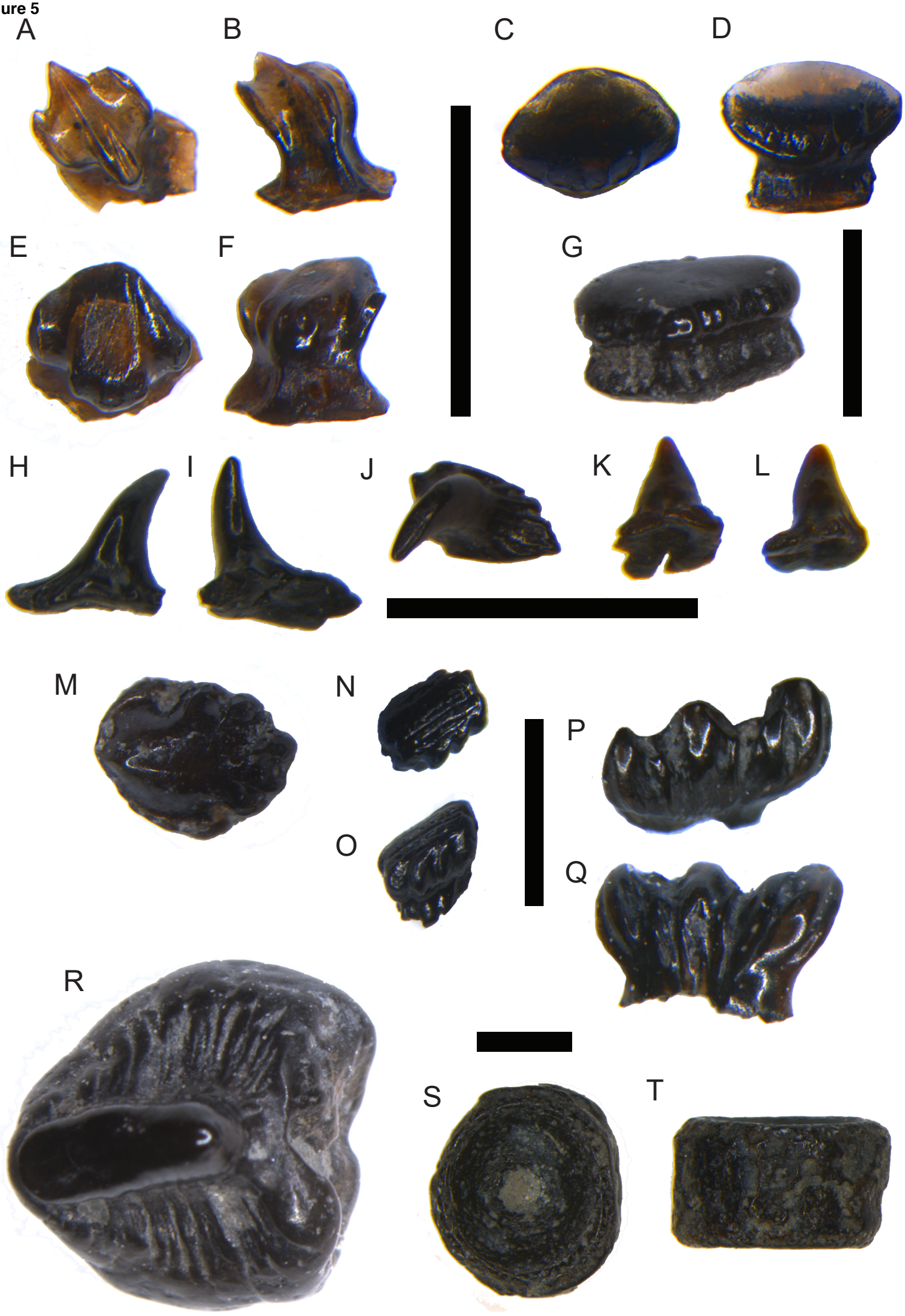

Figure 6

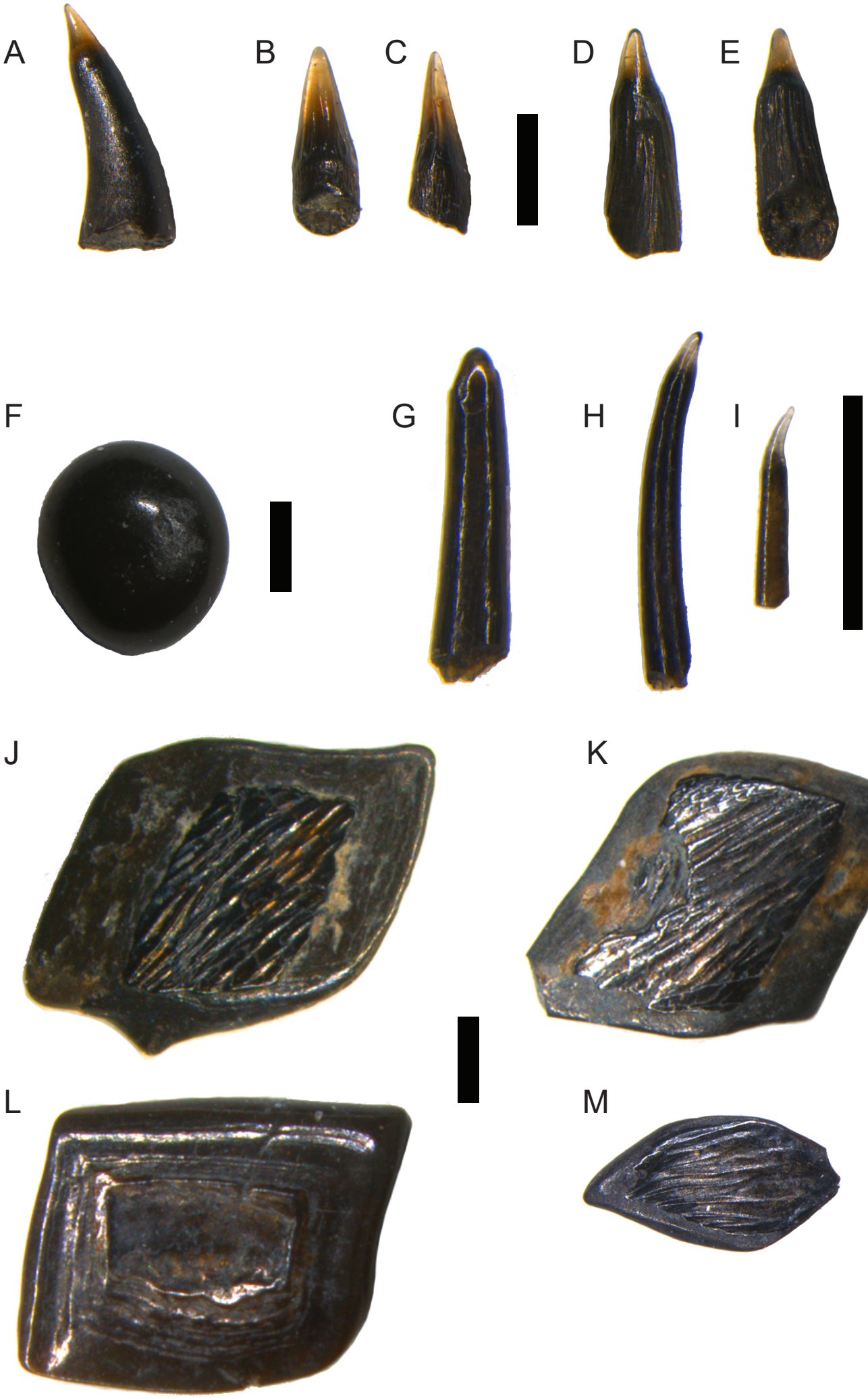

Figure 7

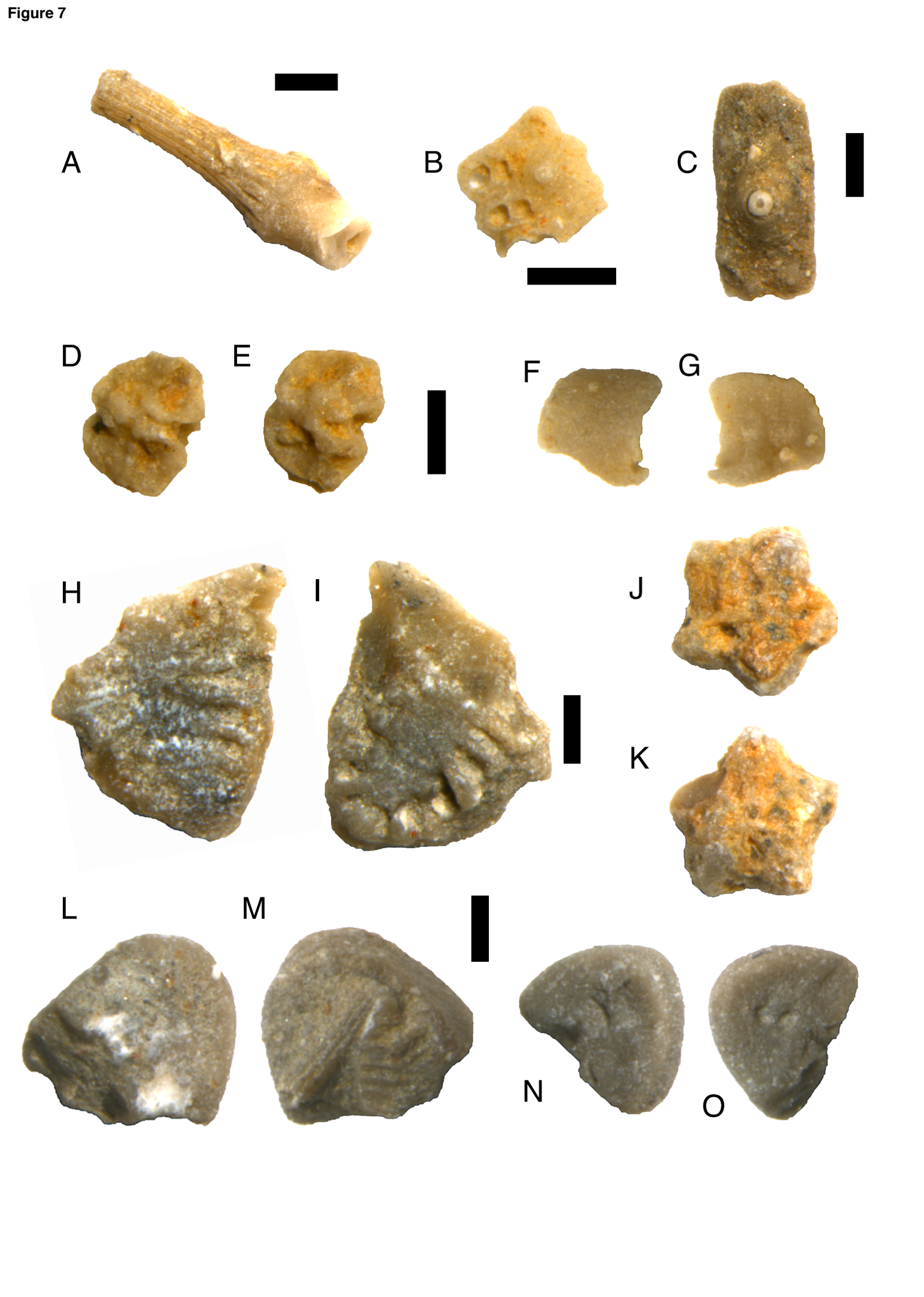

Figure 8

Figure 9

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